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LETHAL AND NON-LETHAL PARASITOIDS OF *PLATYPREPIA VIRGINALIS* (ARCTIIDAE)

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By definition, a parasitoid is supposed to kill its host (Borror et al. 1989, Ricklefs 1990, Godfray 1994). Previously we reported that *Platyprepia virginalis* Bvd. (Lepidoptera: Arctiidae) caterpillars infected with parasitoids of *Thelaira americana* Brooks (Diptera: Tachinidae) (formerly called *T. bryanti*) often survived the emergence of their flies (English-Loeb et al. 1990, 1993, Karban & English-Loeb 1997). At our study site at the Bodega Marine Reserve, Sonoma County, California (38°19.06′N, 123°4.20′W), caterpillars survived approximately 50% of the time although rates of survival depended upon the host plants and behavior of the caterpillars (English-Loeb et al. 1993, Karban and English-Loeb 1997, Karban 1998). Most early instar *P. virginalis* caterpillars use *Lupinus arboreus* at this study site although *Conium maculatum* is preferred by later instar caterpillars that are parasitized (Karban & English-Loeb 1997). Caterpillars that survive their parasitoids take longer to develop and pupate at slightly smaller weights than unparasitized caterpillars, although they are reproductively viable (English-Loeb et al. 1990, Karban & English-Loeb 1997). We most commonly observe non-lethal parasitism when we rear caterpillars in the field in large sleeve cages; lab rearings are much more likely to be fatal.

Because non-lethal parasitism is an unusual phenomenon (other examples have been reported for tachinids and caterpillars, e.g., Richards & Waloff 1948, DeVries 1984), we conducted a comparative study to determine what features of this system allowed both the caterpillar and its tachinid parasitoid to survive. We found populations of *P. virginalis* in other locations where caterpillars used different host plants to determine if *T. americana* was ever non-lethal under those circumstances. We also reared 316 individuals of *P. virginalis* outdoors in sleeve cages to determine if other, less common, parasitoid species were ever non-lethal to our host population at the Bodega Marine Reserve.

During 1994 we found populations of *P. virginalis* in riparian habitats of the Trinity Alps (along Rush Creek in Trinity County (40° 46.80′N, 122°51.14′W) and along French Creek (40°41.75′N, 122° 38.27′W) and Water Gulch (40°40.08′N, 122°42.20′W) in Shasta County, California). We returned to these sites during April 1995, 1996, and 1997 and caged individuals (50 caterpillars in 1995, 75 in 1996, and 44 in 1997) of this inland race on several host plants that were being used naturally by caterpillars at those locations. Our field rearing techniques are described in detail elsewhere (Karban & English-Loeb 1997).

Of 22 caterpillars that produced adult *T. americana* flies from these inland samples, 10 survived to become adults. This 45% rate of survival is indistinguishable from the 37% survival rate of caterpillars parasitized by *T. americana* during the same three seasons at Bodega (Fisher's exact test, n = 60, p = 0.59). Survival of both caterpillars and flies from this inland (Trinity Alps) population occurred when caterpillars were reared on *C. maculatum* (2 individuals), *Lupinus albicaulis* (1 individual), and especially *Lupinus albifrons* (7 individuals). Caterpillars were also reared on *Rubus ursinus*, a commonly used host plant along Rush Creek; of 3 parasitized individuals reared on this host plant, none survived. Caterpillars were found on other host plants including species of *Plantago*, *Phacelia*, *Nemophila*, *Plagiobothrys*, and *Rumex*, although these were not tested as host plants because single individual plants were not large enough to support the complete development of a caterpillar. These observations indicated that the populations of *P. virginialis* and *T. americana* at the Bodega Marine Reserve were not unique in exhibiting non-lethal parasitism. In addition, species of lupine other than *arboreus* could serve as the sole host plants of late instar caterpillars that survived emergence of parasitoids.

Late instar caterpillars (already containing parasitoid larvae) were reared in field cages at the Bodega site in 1987, 1989, 1990, 1991, 1993, 1994, 1995, 1996, and 1997, and at the Trinity Alps sites in 1995, 1996, and 1997. Parasitoids that they contained pupated in these field cages and were collected. Rates of parasitism at Bodega have ranged from 6% in 1996 to 71% in 1990. Most of the parasitoids were *T. americana*, although occasionally other species were recovered. We have 5 rearings of *Carcelia reclinata* (A&W), a second tachinid, from *P. virginalis* in the Trinity Alps. This parasitoid was common at our populations in the Trinity Alps in 1994, although we did not rear caterpillars in outdoor cages that season. *C. reclinata* has also been reared from our Bodega population at least 1 time. We reared *Leschenaultia adusta* (Wulp), a very large tachinid, from individuals in our Bodega population on 5 different occasions. We also reared eight individuals of a large ichneumonid wasp, *Ichneumon* sp. from caterpillars at Bodega and from Shasta and Trinity counties. In no case (n = 18), did caterpillars recover to pupate successfully after emergence of *C. reclinata*, *L. adusta* or *Ichneumon* sp. During this same period of time (1995–97), 45% of caterpillars with *T. americana* survived to become viable adult moths (n = 22). Given the same rate of survival after emergence of *T. americana*, we would have expected 8 caterpillars to have recovered after emergence of the other parasitoids. The likelihood that recovery rates are as high following emergence of these other parasitoids (considered together) as it is following *T. americana* is 0.001 (Fisher's exact test). These results suggest that there is something unique about the interaction between *P. virginalis* and *T. americana* that allows for non-lethal parasitism.

Of these three less common parasitoids, *C. reclinata* seems the most likely candidate to be non-lethal. Because of the low sample size (n = 5) of observations of this parasitoid, the likelihood that recovery rates following emergence of *C. reclinata* differ from those of *T. americana* are only 0.12 (Fisher's exact test). More observations of *C. reclinata* parasitizing *P. virginalis* are necessary to determine whether *C. reclinata* can be non-lethal.

What factors could allow *T. americana* but not the other parasitoids to be non-lethal to *P. virginalis*? The ichneumonid is much larger than *T. americana* and remains in the host for longer, often (3 of 8 cases) emerging from the pupa. Lepidopteran larvae sometimes live for days or weeks after emergence of hymenopteran parasitoids although they invariably perish before successfully reproducing (Clausen 1962, Strand et al. 1988). (Hymenopteran parasitoids are much better studied than dipteran parasitoids [Feener and Brown 1997]). Recovering after emergence of *L. adusta*, another tachinid, seems about as unlikely as recovering after the ichneumonid. Like the ichneumonid, *L. adusta* is very much larger than *T. americana* and emerges later, often when the host is beginning to spin its cocoon (3 of 4 cases). *C. reclinata* is a smaller tachinid and can complete its development relatively rapidly. However, in 3 of the 5 cases in which we observed *C. reclinata*, this parasitoid emerged from a caterpillar that was spinning its cocoon. We have noted that the chances that *P. virginalis* will survive the emergence of *T. americana* decrease the later in the development of the caterpillar that parasitoid emergence occurs. One difference between *T. americana* and the other parasitoids that are always lethal is that *T. americana* often completes development during one of the middle stadia of the host larva.

It may be informative to consider the differences from the perspective of the parasitoid's life history traits. Belshaw (1994:149) describes two developmental strategies for tachinids. Some species, perhaps including the ichneumonid and *L. adusta*, delay their own development and only kill their host close to pupation. Selection on these species presumably favors individuals that maximize their size at pupation by consuming most or all of the host. These species will always be lethal. Belshaw describes other tachinids that develop rapidly, often restricting their attack to late instars. *C. reclinata* may fall into this category. Selection on this species presumably favors speed of development or early emergence at the expense of not exploiting all of the host. *T. americana* does not fit this category perfectly because it develops quickly although it attacks early instars. This suggested that *T. americana* that develop rapidly may be more fit than those that take longer. A reanalysis of pupal weights of *T. americana* that developed in *P. virginalis* at Bodega Bay (methods

and data in Karban & English-Loeb 1997) revealed that those that completed development earlier in the season were markedly heavier than those completing development later ($F_{1,76} = 25.037$, $p < 0.001$). This result is consistent with the hypothesis that selection for rapid development at the expense of incomplete host exploitation may sometimes produce non-lethal parasitism. It would be informative to examine whether other tachinids that develop rapidly are also non-lethal.

In conclusion, there does not seem to be anything special about the populations of *P. virginalis*, *T. americana* or the host plants used at Bodega Bay. Non-lethal parasitism was observed for other populations of these insects. However, *T. americana* does appear to be unique among the four parasitoids that attack *P. virginalis* in allowing the host to recover and eventually reproduce. Hopefully these comparisons can be used in the future to elucidate the nature of the interactions that determine lethal and non-lethal parasitism.

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